Yield- and biomass-per-recruit analysis for rotational fisheries, with an application to the Atlantic sea scallop (*Placopecten magellanicus*)

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Abstract—A general model for yield-per-recruit analysis of rotational (periodic) fisheries is developed and applied to the sea scallop (*Placopecten magellanicus*) fishery of the northwest Atlantic. Rotational fishing slightly increases both yield- and biomass-per-recruit for sea scallops at F_{MAX}. These quantities decline less quickly when fishing mortality is in-creased beyond F_{MAX} than when fishing is at a constant rate. The improvement in biomass-per-recruit appears to be nearly independent of the selectivity pattern but increased size-at-entry can reduce or eliminate the yield-per-recruit advantage of rotation. Area closures and rotational fishing can cause difficulties with the use of standard spatially averaged fishing mortality metrics and reference points. The concept of temporally averaged fishing mortality is introduced as one that is more appropriate for sedentary resources when fishing mortality varies in time and space.

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There has been growing interest in using rotational fishing to manage sessile or sedentary stocks (e.g. Caddy and Seijo, 1998). Under such a strategy, fishing mortality in a given area is varied periodically. Typically, the area is closed for a period of time, then fished, and then closed again. The openings of the different areas are timed so that at least one area is open to fishing each year. This approach has been proposed or is being used for abalone, corals, sea cucumbers, geoduck clams, sea urchins, and several species of scallops (Sluczanowski, 1984; Garcia, 1984; Botsford et al., 1993; Caddy, 1993; Heizer, 1993; Campbell et al., 1998; Caddy and Seijo, 1998; Lai and Bradbury, 1998).

Recently, area closures have been used to help manage the Atlantic sea scallop (*Placopecten magellanicus)* fishery off the northeastern United States. Three areas on Georges Bank were closed to scallop and groundfish fishing in December 1994 to help protect depleted groundfish resources. Subsequently, there have been substantial increases in scallop abundance, biomass, and mean size in these areas; mean scallop biomass in the closed areas, as measured by the Northeast Fisheries Science Center (NEFSC) sea scallop survey, rose from 0.6 kg/tow in 1994 to 15.8 kg/tow in 2000.[1] During limited openings of these areas to fishing in 1999 and 2000, nearly 5000 metric tons (t) of scallop meats (about 20% of the total landings during this period) were landed, while biomass levels remained high. In April 1998, two areas in the Mid-Atlantic Bight were closed to scallop fishing for three years in order to protect high concentrations of juvenile scallops. Scallop biomass has increased markedly since the closures in these areas as well, from 0.8 kg/tow in 1997 to 9.7 kg/tow in 2000[1] and about 3500 t of scallop meats have been landed in these areas in the year since they were reopened in May 2001. These data suggest that temporary or rotational closures can help increase scallop biomass and yield. For these reasons, a rotational management system for the U.S. Atlantic sea scallop fishery is currently under consideration.

Many common fisheries models may not be appropriate for sessile stocks because these models assume spatially uniform fishing mortality (Caddy, 1975). Such a "dynamic pool" assumption is strongly violated when a sessile stock is fished rotationally so that a portion of the stock is not fished in a given year. For this reason, many previous analyses of rotational fisheries have used either spatially explicit simulations (e.g. Caddy and Seijo, 1998), per-recruit analyses of pulse fishing, where all vulnerable individuals are removed from an area when the area is fished (e.g. Sluczanowski, 1984), or per-recruit analyses of a single cohort (e.g. Gribble and Dredge, 1994). Spatially explicit models suffer from their complexity, making it difficult to extract general principles from model

[1] NEFSC (Northeast Fisheries Science Center). 2001. Report of the 32nd northeast regional stock assessment workshop (32nd SAW). Stock Assessment Review Committee (SARC) consensus summary of assessments. NEFSC Ref. Doc. 01-05, 289 p. [Available from NEFSC, 166 Water St., Woods Hole MA 02543.]

simulations. Analysis of pulse fishing, although simple to apply and understand, is not applicable to those situations where only a portion of the available resource is removed when an area is opened periodically to fishing. Per-recruit analysis of a single cohort is not applicable to relatively nonselective multiple age-group fisheries.

Botsford et al. (1993) developed a mixed-age rotational yield-per-recruit model for red sea urchins. They showed that rotational fishing for these urchins would increase egg production considerably, while slightly decreasing yield-per-recruit. Recently, Myers et al. (2000) presented a mixed-age per-recruit analysis of a possible rotational fishery strategy for sea scallops. The emphasis of this study was on the effect of putative high levels of indirect (noncatch) fishing mortality on yield-per-recruit, and on a proposed rotational plan that Myers et al. suggested would help ameliorate this effect.

The purpose of the present article is to present a general theory for any type of periodic or rotational fishing strategy for a mixed-age sessile or sedentary stock. This work generalizes many of the above mentioned studies (in particular, that of Botsford et al., 1993) and does not require an assumption of constant recruitment or specific spatial configuration (or both). This theory is applied to the Atlantic sea scallop fishery of Georges Bank.

Measures of fishing mortality and overfishing definitions are usually based on models where fishing is assumed constant in space and time. In rotational fisheries, or in cases where part of a fishing ground has been closed indefinitely to fishing, these assumptions may be seriously violated, especially for stocks that are relatively immobile. Alternative measures of fishing effort and overfishing definitions are presented here that are more appropriate to fisheries of nonmobile stocks where rotational or indefinite closures are used.

Methods

The object of this analysis was to compute the expected yield-per-recruit and biomass-per-recruit of a cohort located in an area where fishing mortality may depend on the year and the variation in fishing mortality is periodic with time. Rotational fishing is usually thought of as a sequence of periodic closures and openings of different areas. The theory described here is more general, and can be applied to any situation where fishing mortality is varied periodically in a given area.

Suppose the fully recruited fishing mortality in an area during year k is F_k and that fishing mortality rates vary periodically with period p (where p is in years), so that $F_{p+k} = F_k$ for all k. Let F_{AVG} be the mean of $F_1,F_2,\ldots,F_p$. For simplicity, it is assumed that there is one recruitment event and one new cohort per year. However, extension of the theory to multiple cohorts per year is straightforward.

There are p possible patterns of fishing mortality experienced by a cohort, depending on the point of the cycle when it enters the fishery. The cohort that enters in the first year will experience fully recruited fishing mortality rates:

$$F_1, F_2, F_3, \ldots, F_p, F_1, F_2, F_3 \ldots \quad (1)$$

during successive years. The next cohort will experience the same fishing mortality rates, but in a different order:

$$F_2, F_3, F_4, \ldots, F_p, F_1, F_2, \ldots \quad (2)$$

and so on.

Two special cases are of particular interest: pulse rotation and symmetric rotation. Pulse rotation means that $F_k = 0$ for k=1,2,...,p–1 (the area is closed for p–1 years), then F_p>0 (the area is pulse fished for one year), and then F_k=0 for k=p+1, p+2,..., 2p–1 (the area is closed again), etc. Symmetric rotation, where p is even, means that $F_k = 0$ for $1 \le k \le p/2$, and $F_k = 2F_{\mathrm{AVG}}$ for $p/2 < k \le p$, i.e. the area is closed for p/2 years and then fished at a constant rate for the next p/2 years.

For each of the p patterns of fishing mortality, yield- and biomass-per-recruit can be calculated by using standard per-recruit techniques. Here, a method similar to the "generic per-recruit" model described in Quinn and Deriso (1999) is used (see Appendix). The only unusual aspect is that the mortality terms Z and F_c in Equations 11–13 (see Appendix) depend explicitly on time, i.e. on the year of the rotational cycle. Each of the p cohorts will have different yield-per-recruit $Y_1,Y_2,\ldots,Y_p$, and biomass-per-recruit $B_1,B_2,\ldots,B_p$ values because the ages at which they experience the fishing mortalities $F_1,F_2,\ldots,F_p$ are different.

Define Y_{AVG} and B_{AVG} to be the means of the p patterns of cohort yield- and biomass-per recruit, respectively. Y_{AVG} is the expected yield of a recruit chosen randomly with respect to cohort. In other words, Y_{AVG} is the long-term mean yield-per-recruit that can be expected from the rotational fishing strategy. Similarly, B_{AVG} is the expected long-term mean biomass-per-recruit. Note that unlike conventional per-recruit theory, yield- and biomass-per-recruit vary with cohort, so that the mean yield- and biomass-per-recruit obtained at any point in time may be different from Y_{AVG} and B_{AVG}.

Let $Y^{(1)},Y^{(2)},\ldots,Y^{(p)}$ be yield-per-recruit of the p cohorts, in decreasing order, so that $Y^{(1)}$ is the highest yield-per-recruit out of all the p cohorts and $Y^{(p)}$ the lowest. $Y^{(1)}$ is an upper bound on the yield-per-recruit that might be obtained with a rotational strategy if, for example, the closure pattern were timed to optimize yield-per-recruit from a large year class.

It is important when comparing rotational and constant fishing strategies to compare alternatives that have the same long-term survival rates, i.e the same natural mortalities and mean fishing mortality rates. If this is not done, then effects of rotation can be confounded with those due to variations in fishing mortalities. If there are initially N_0 fully recruited individuals in an area that are fished at a constant rate F_u, then there will be

$$N_p = N_0 \exp(-pM - pF_u) \quad (3)$$

of these individuals remaining alive after p years. If instead, fishing mortality was varied on a p year rotation, so that in each year of the cycle, fishing mortality in an

Table 1

Estimated life history parameters for Georges Bank sea scallops. Von Bertalanffy growth parameters are from Serchuk et al. (1979). Relations of shell height (SH) to meat weight (MW) (see Eq. 7) were obtained by combining the data of Serchuk and Rak[1] with that of NEFSC (Footnote 2 in the general text). The natural mortality estimate is from Merrill and Posgay (1964). The selectivity pattern is based on the current gear configuration of scallop dredges with 89-mm rings (NEFSC, Footnotes 1 and 2 in the general text).

	K (/yr) (growth)	L_∞ (mm) (growth)	M (/yr) (natural mortality)	a (ln g) (SH/MW parameter)	b (SH/MW parameter)	$h_{\min}$ (mm) (Min SH selected)	h_{full} (mm) (SH for full selectivity)	h_d (mm) (cull size)	d (discard mortality)
Value	0.3374	152.46	0.1	–11.6038	3.1221	65	88	75	0.2

[1] Serchuk, F. M., and R. S. Rak. 1983. Biological characteristics of offshore Gulf of Maine scallop populations: size distribution, relations of shell height to meat weight, and relative fecundity patterns. Reference document 83-07, 42 p. [Available from Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.]

area is given by $F_1, F_2, , F_p$, respectively, then the number of individuals remaining alive after p years would be

$$N_p^* = N_0 \exp\left(-pM - \sum_{i=1}^{p} F_i\right). \quad (4)$$

In order for the long-term survivorship of the two strategies to be equal (i.e., N_p=N_p^*), the uniform fishing mortality F_u must equal the average fishing mortality

$$F_{AVG} = \frac{1}{p}\sum_{i=1}^{p} F_i \quad (5)$$

of the rotation plan. Therefore, F_{AVG} is used to scale all the graphs and per-recruit comparisons.

The model described above and in the Appendix was implemented as a Fortran-90 program where the integrals were numerically computed with a time step of 0.01 y. Parameters used in the model are given in Table 1 and represent estimates for growth and mortality of Atlantic sea scallops (*Placopecten magellanicus)*, for which rotational management is currently under consideration.

Results

Yield-per-recruit curves for no rotation (continuous uniform fishing), three-year pulse rotation (i.e. the area is closed for two years and fished for one year), six-year pulse rotation, and nine-year pulse rotation are given in Figure 1. Note that the x axis in Figure 1 is the mean fishing mortality rate F_{AVG}, and the y axis is mean (i.e. expected) yield-per-recruit Y_{AVG}, averaged over cohorts. Because the mean fishing mortality rate is the same for all points at the same x coordinate, the three-year rotation has a fishing mortality rate during years when fishing occurs (F_p) that is three times as high, and the six-year rotation six times as high, as the constant F (no rotation) strategy with the same F_{AVG}.

Rotation affects the yield-per-recruit curve for sea scallop in three different ways (see Fig. 1). First, rotation modestly increases the maximum mean yield-per-recruit Y_{MAX}; the maximum mean yield-per-recruit for the nine-year rotation is about 9% greater than without rotation. Second, F_{MAX} (i.e. the value of F_{AVG} where Y_{MAX} is obtained) increases somewhat under rotation, especially for longer rotation periods. Third, there is less yield penalty in rotational management for exceeding F_{MAX}. For example, fishing at F = 1 results in a 38% loss of yield if there was no rotation, but only an 8% loss under a six-year pulse rotation. Although 6-yr pulse rotation results in only a 5% increase in yield-per-recruit over no rotation at their respective F_{MAX} values, the advantage of 6-yr pulse rotation at F = 1 is 43%.

Maximum yield-per-recruit for pulse fishing as a function of the rotation period p is shown in Figure 2. The best yield-per-recruit is obtained for long periods of 9 to 10 years. However, this type of strategy would imply that a number of years would pass before any yield would be obtained from most recruits and this strategy would only slightly increase maximum yield-per-recruit over that of steady fishing. Depending on management goals, it might be reasonable to discount future yields, so that the present value of yield taken t years into the future would be discounted by $\exp(-\delta t)$, where δ is the annual discount rate (assumed 10%/yr). The rotation period that maximizes discounted yield-per-recruit is 6 years (Fig. 2). If prices as a function of meat weight are known, it would also be possible to do a similar analysis to maximize discounted value-per-recruit.

Yield isopleths, commonly used to visualize yield-per-recruit analysis (Beverton and Holt, 1957), are given in Figure 3A (yield-per-recruit) and 3B (discounted yield-per-recruit). For rotational analyses, fishing mortality is placed on the x-axis and rotational period on the y-axis. Note again that for longer rotation times, the decline in yield for fishing mortalities greater than F_{MAX} is much less than without rotation. The value of F_{MAX} and maximum yield-per-recruit increases slightly with longer rotation periods.

Biomass-per-recruit for no rotation, 3-, 6- and 9-yr pulse rotation strategies is given in Figure 4. Compared to constant fishing, rotational fishing gives increased biomass-per-recruit; this increase is most evident for the longer

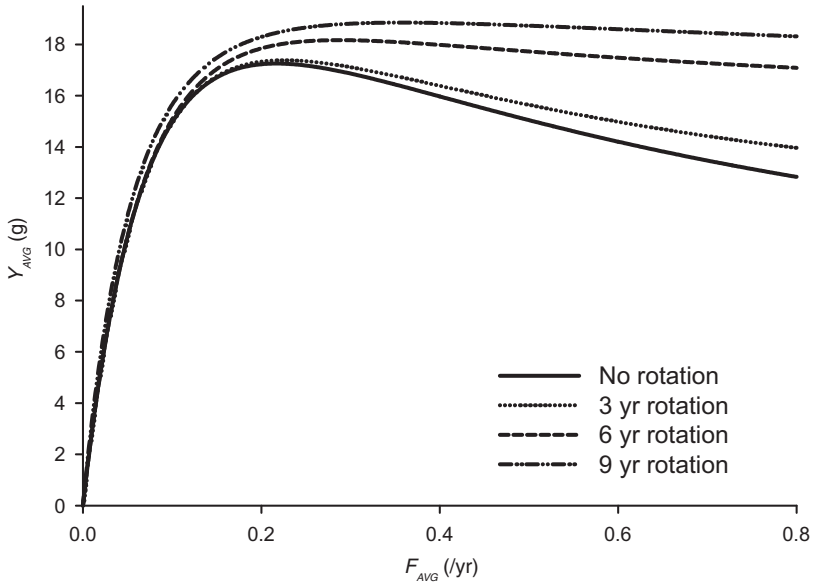

Figure 1

Yield-per-recruit curves for Georges Bank sea scallops with no rotation and with 3-, 6-, and 9-yr pulse rotations.

rotations and higher fishing mortalities. At F_{MAX}, the increase in biomass-per-recruit is slight, unless a very long (e.g. 9-yr) rotational period is employed.

The performance of rotation can be assessed as a function of selectivity at size. Figure 5A gives maximal yield-per-recruit for a number of pulse rotation strategies and a variety of values of h_{min}, the smallest size selected by the gear; the size of full selectivity, h_{full}, was taken as h_{min} + 23 mm (consistent with the assumed current gear selectivity pattern; see Table 1). Rotation can give substantial yield-per-recruit advantages when the gear selects animals of well below optimal size, especially for longer periods. However, long-period rotation actually gives less yield-per-recruit than constant fishing for larger values of h_{min}. Figure 5B gives a similar plot for biomass-per-recruit, where fully recruited fishing mortality is fixed at F = 0.3 in all cases. Unlike yield-per-recruit, rotational fishing increases biomass-per-recruit regardless of the selectivity pattern, especially when the rotational period is long.

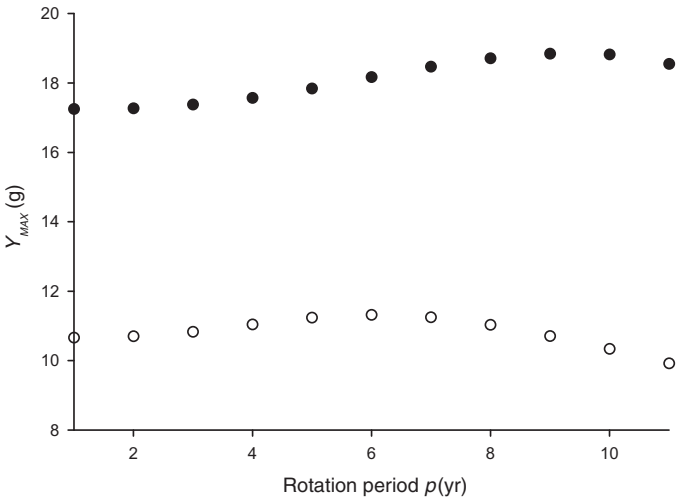

Figure 2

Maximum yield-per-recruit (solid circles) and discounted (10%) yield-per-recruit (open circles) for Georges Bank sea scallops with a pulse rotation of periods between 1 and 11 years.

Yield-per-recruit from different cohorts under a rotational system can vary considerably. The cohort which recruits into the fishery at about the time of the closure produces the highest yield-per-recruit, whereas the cohort that reaches exploitable size at about the time that the area is opened has the lowest. Figure 6 gives the mean yield-per-recruit together with that of the cohorts with the highest and lowest yield-per-recruit under six-year pulse rotational management (i.e. Y_{AVG}, $Y^{(1)}$, and $Y^{(6)}$, respectively). A 31% increase in maximal yield compared to constant fishing (and 25% increase over the average yield-per-recruit under rotation) can be obtained from the cohort whose yield-per-recruit is the highest under rotation. Note that, unlike conventional yield-per-recruit curves for sea scallops, yield-per-recruit from this cohort is almost completely insensitive to effort beyond a certain level.

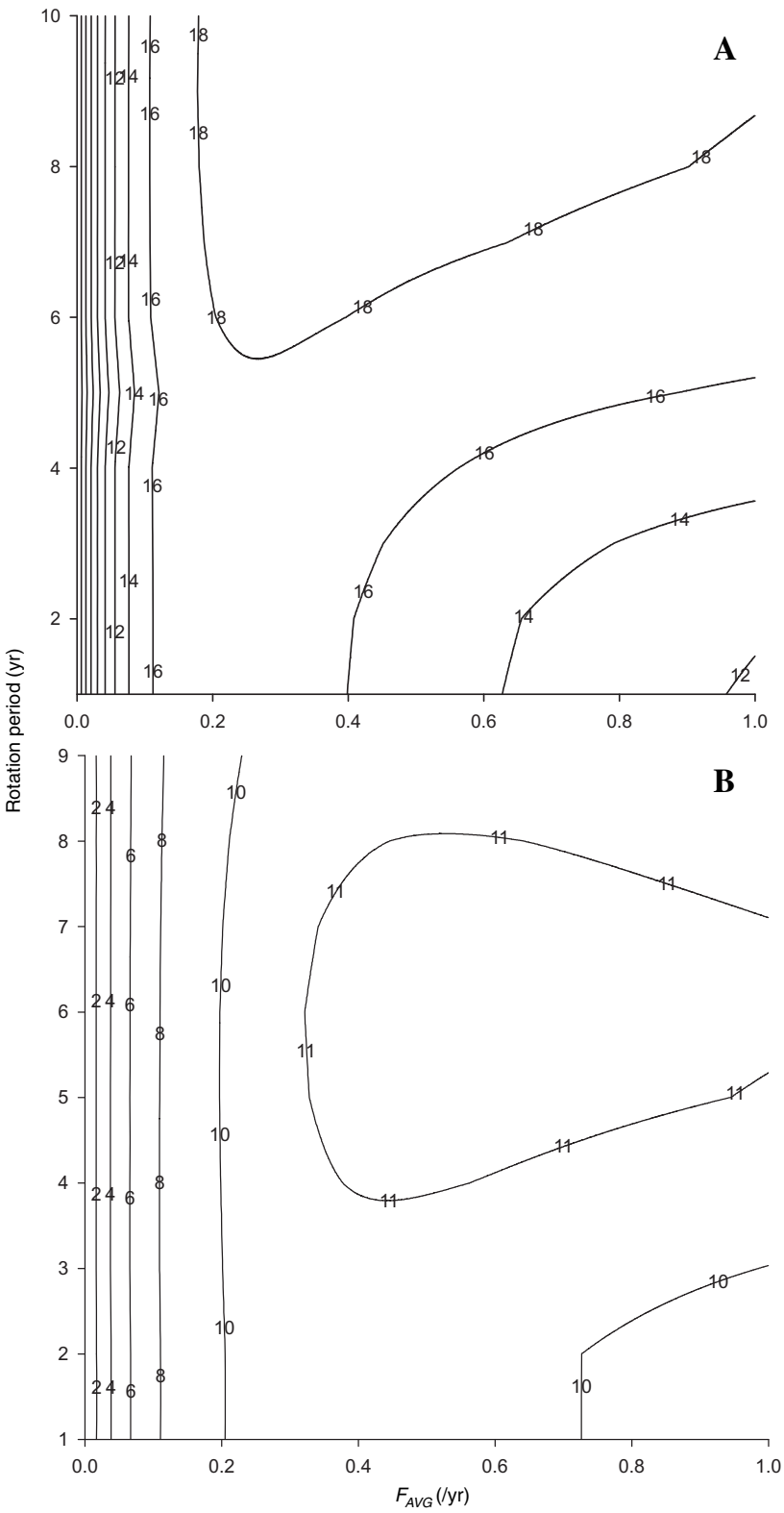

Figure 3

Yield-per-recruit (**A**) and discounted (10%) yield-per-recruit (**B**) isopleths for Georges Bank sea scallops with pulse rotation. Note that the *y* axes represent rotation period.

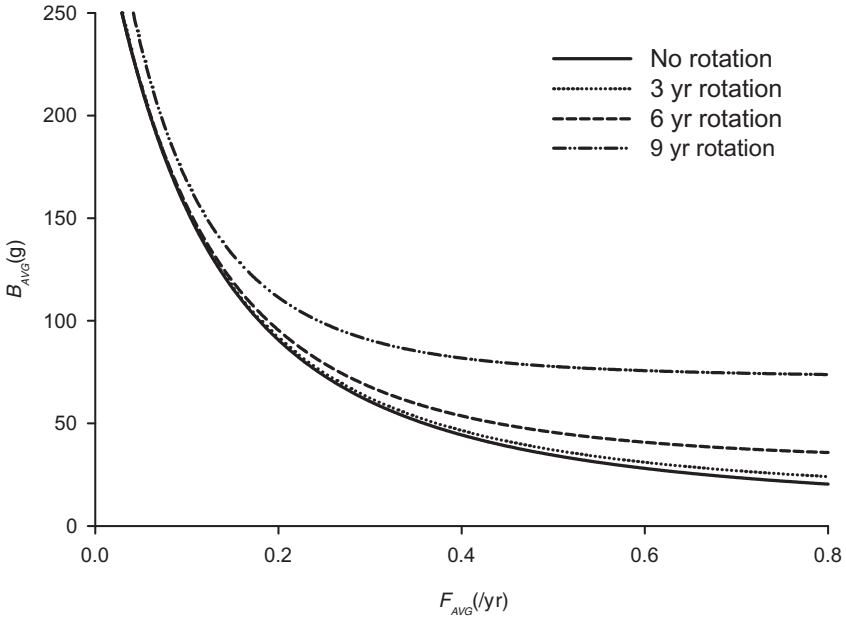

Figure 4

Biomass-per-recruit for Georges Bank sea scallops with no rotation and with 3-, 6-, and 9-yr pulse rotations.

Table 2

Calculated values of F_{MAX}, Y_{MAX}, B_{MAX}, and discounted (*Dsc*) Y_{MAX} (in grams, with a 10% discounting factor) for (**A**) pulse rotation with no incidental fishing mortality, (**B**) pulse rotation with 15% incidental fishing mortality, and (**C**) symmetric rotation with no incidental fishing mortality. p = period of rotation.

	p	F_{MAX}	Y_{MAX}	B_{MAX}	*Dsc* Y_{MAX}		p	F_{MAX}	Y_{MAX}	B_{MAX}	*Dsc* Y_{MAX}
A	1	0.217	17.25	84.0	10.66	**B (cont.)**	4	0.205	14.81	88.4	9.01
	2	0.219	17.27	83.6	10.70		5	0.219	14.99	85.4	9.16
	3	0.225	17.38	82.4	10.83		6	0.236	15.20	82.8	9.25
	4	0.239	17.57	79.6	11.04		7	0.257	15.43	81.2	9.25
	5	0.259	17.84	76.8	11.24		8	0.277	15.63	82.2	9.15
	6	0.287	18.17	74.5	11.32		9	0.292	15.75	86.0	8.96
	7	0.324	18.47	73.8	11.25		10	0.300	15.8	91.8	8.70
	8	0.351	18.71	77.4	11.03		11	0.302	15.75	99.0	8.4
	9	0.363	18.84	84.2	10.71	**C**	2	0.219	17.27	83.6	10.70
	10	0.372	18.82	92.0	10.34		4	0.225	17.4	82.5	10.82
	11	0.374	18.69	100.6	9.93		6	0.235	17.56	81.0	10.90
B	1	0.192	14.62	91.9	8.79		8	0.244	17.68	81.1	10.85
	2	0.193	14.62	91.6	8.80		10	0.248	17.73	83.5	10.68
	3	0.197	14.68	90.5	8.88		12	0.253	17.64	86.3	10.44

Yield-per-recruit curves for 6-yr symmetric rotation (i.e. closed for three years and then opened for three years), 10-yr symmetric rotation, 6-yr pulse rotation, and no rotation are given in Figure 7. Symmetric rotation gives yields-per-recruit that lie between that of pulse rotation and constant fishing. Maximum yield-per-recruit, together with the associated B_{MAX}, and maximal discounted yield for pulse rotation, with and without 15% incidental mortality, and for symmetric rotation without incidental mortality, are given for various rotation periods in Table 2.

Results from yield-per-recruit runs with incidental fishing mortality (Table 2B) show similar patterns to

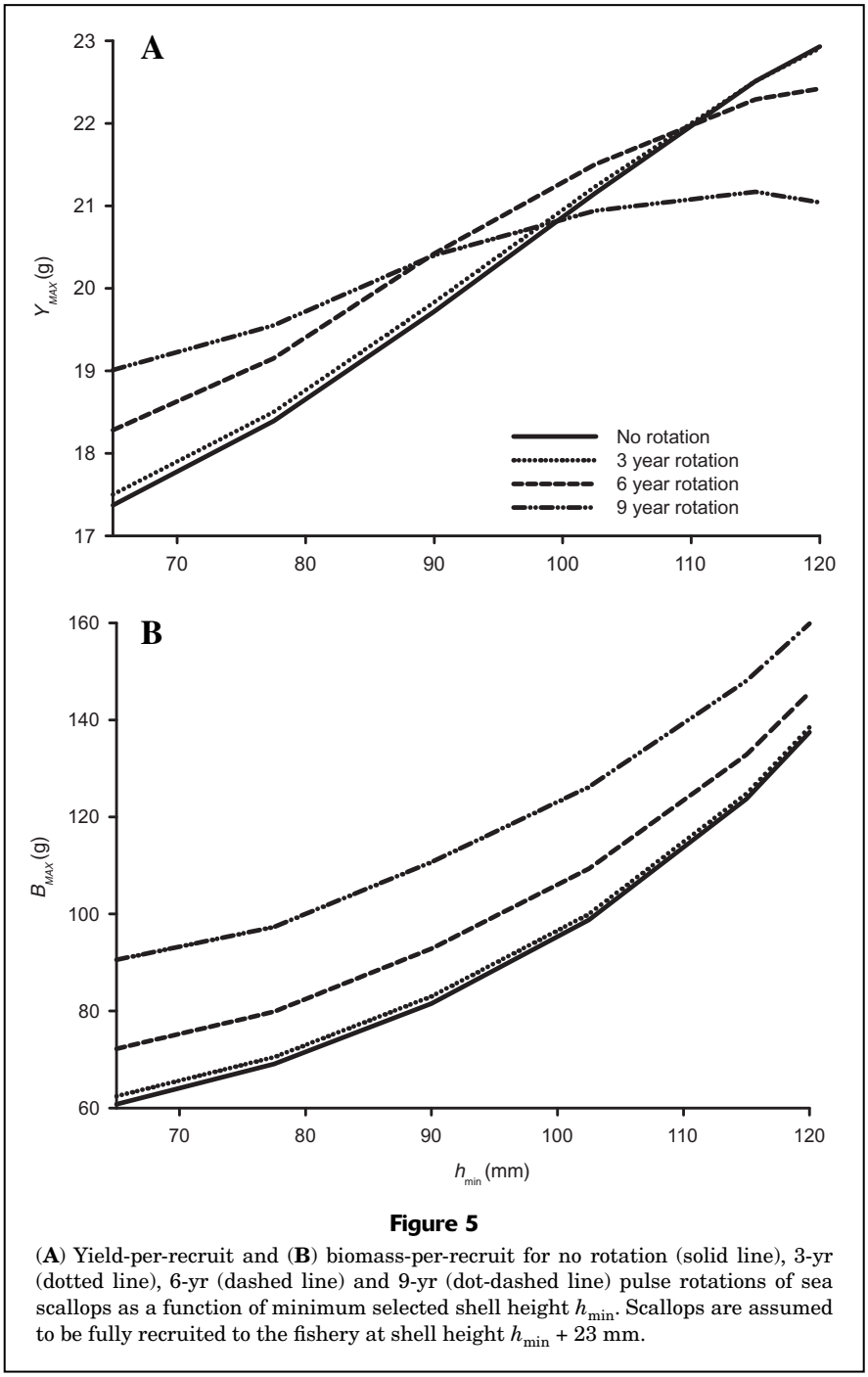

Figure 5

(**A**) Yield-per-recruit and (**B**) biomass-per-recruit for no rotation (solid line), 3-yr (dotted line), 6-yr (dashed line) and 9-yr (dot-dashed line) pulse rotations of sea scallops as a function of minimum selected shell height $h_{\min}$. Scallops are assumed to be fully recruited to the fishery at shell height $h_{\min}$ + 23 mm.

results with no incidental fishing mortality (Table 2A). Note that both yields and the value of F_{MAX} are reduced if incidental fishing mortality exists and that the penalty for overfishing without rotation is somewhat higher (about 67% loss in yield-per-recruit for fishing at F=1 without rotation compared to 38% without incidental mortality). However, at F_{MAX}, the loss of yield due to incidental mortality is about the same for rotational fishing as for steady fishing.

Discussion

Rotational fishing can generate increased yield- and biomass-per-recruit for sea scallops compared to nonrotational fishing. The expected increase in maximum yield-per-recruit is modest (<10%) for a fixed rotational pattern. The over 30% gain in yield-per-recruit obtained from cohorts that reached exploitable size near the time of the closure is partially cancelled by the loss of yield-per-recruit

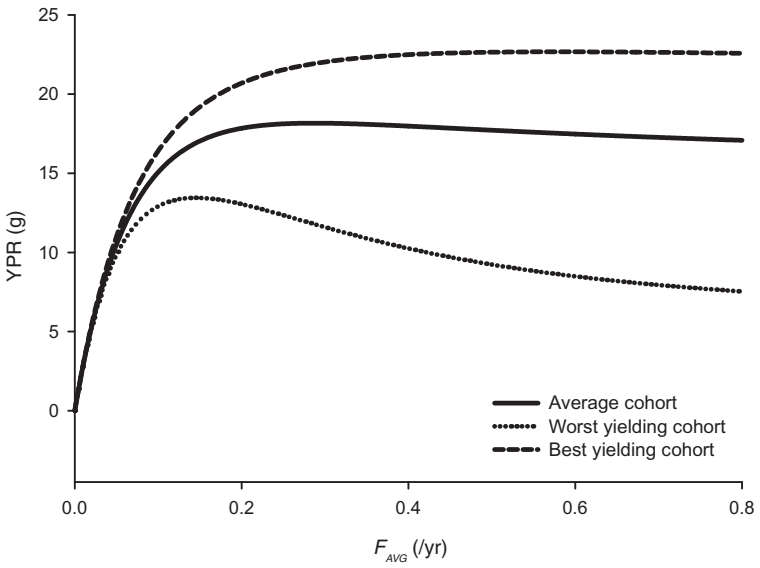

Figure 6

Yield-per-recruit for a 6-yr pulse rotation of Georges Bank sea scallops from an average cohort, and those that benefit the most and the least from rotation.

on those cohorts that reached exploitable size at about the time the area was reopened, thereby resulting in only a modest gain in yield-per-recruit. A more substantial gain in maximum yield-per-recruit (up to 30% greater than constant fishing) can be obtained if the closure is timed to optimally exploit an unusually large year class. These results are consistent with several studies that indicate that periodic fishing can often increase yields over constant fishing (Botsford, 1981; De Klerk and Gatto, 1981; McCallum, 1988; Clark, 1990; Myers et al., 2000).

A second, and perhaps more important, advantage of rotational fishing is that it alleviates the impact of both growth and recruitment overfishing. Growth overfishing (i.e. fishing at a level higher than F_{MAX}) under rotational management induces a substantially smaller reduction in yield-per-recruit than would occur with constant fishing. Rotation also increases biomass-per-recruit for sea scallops, especially for levels of F above F_{MAX}, thereby reducing the impact of possible recruitment overfishing. It might be argued that overfishing should not be occurring in any case. However, even when management measures are taken to eliminate overfishing, it can still occur, for example, if 1) reference points are incorrect because of uncertainty in life history parameters; 2) fishing mortality, or the effect of management measures on fishing mortality, has been underestimated; or 3) there is localized overfishing because of spatial variation in fishing intensities or life history parameters (or variation in both), even though when averaged spatially, $F_{AVG} \leq F_{\mathrm{MAX}}$ (Caddy, 1975; Hart, 2001). Rotational fishing can thus be thought of as part of a precautionary strategy. In so much as it may increase maximum yield, rotational management is superior to many other precautionary measures that reduce yield. The only costs of rotational management are the costs of administrating and enforcing such a system, and socioeconomic costs from temporary closures of traditional fishing grounds. The latter might be significant if closures force fishermen to make long distance steams to unfamiliar areas. Because the optimal F_{AVG} under rotation is only slightly greater than the nonrotational F_{MAX}, the amount of effort and fleet capacity required to optimize yield-per-recruit under rotation is about the same as that needed under uniform fishing.

Rotation also imposes practical constraints on the level of average fishing effort, thereby limiting the extent to which stocks can be overfished. Fishing mortality rates for U.S. sea scallop stocks were estimated as exceeding 1.0/yr during the late 1980s and early 1990s.[1] This would correspond under a 6-yr pulse rotation to an unaveraged fishing mortality of over $F = 6$ in the area open to fishing. Such a high fishing morality rate, corresponding to about a 98% exploitation rate for fully recruited scallops, is likely to be impractical for both physical and economic reasons. Thus, F_{AVG} in a rotation plan would likely be considerably below the high levels seen in the late 80s and early 90s, even if there was no other restriction on fishing effort other than pulse rotation.

Myers et al. (2000) claimed that "near-optimal yields are achieved across a wide range of fishing mortalities" in their rotational scheme. However, much of their analysis was confounded by their use of unaveraged open area fishing mortality ($=pF_{\mathrm{AVG}}$) on the x axis of their per-recruit curves. For example, in the case analyzed in Myers et al (2000), where one of p areas would be fished each year, the fishing mortality F applied in the area open to fishing in a 9-yr rotation (i.e. 1/9 of the area would be fished each

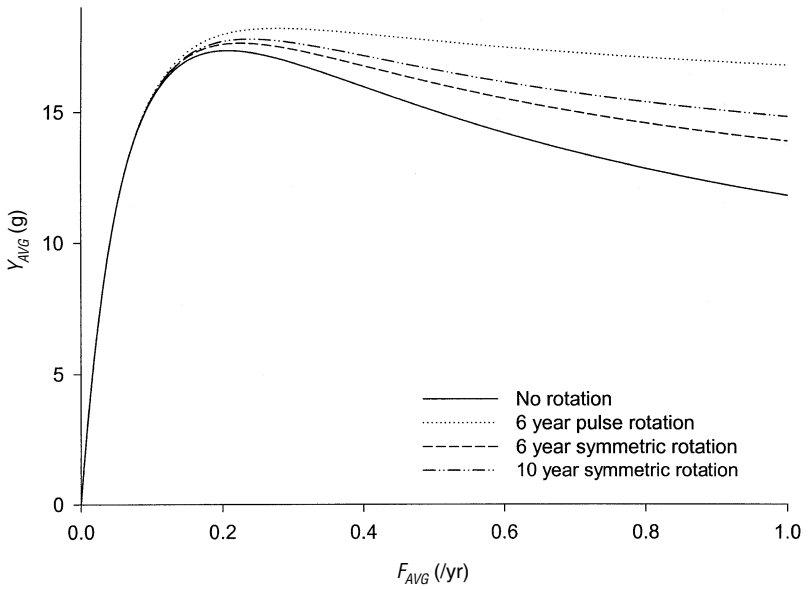

Figure 7

Comparison of yield-per-recruit for Georges Bank sea scallops with 6-year and 10-year symmetric rotations with that of a 6-yr pulse rotation or no rotation.

year and that $F = F_{AVG}/9$) would represent one ninth of the actual effort as the same F applied to the whole area under non-rotational fishing. Use of unaveraged fishing mortality has the effect of stretching the x axis by a factor of p, thereby making their graphs appear flatter than they actually are. F_{AVG} is representative of not only the true time-averaged fishing mortality but also in many cases would be proportional to spatially averaged fishing effort (as measured by, e.g., hours fished).

Myers et al. (2000) also suggested that rotational fishing would help lessen the impact of indirect (incidental) fishing mortality on yield-per-recruit. The analysis given in the present study indicates that incidental mortality lowers yield-per-recruit at F_{MAX} about the same amount regardless of whether or not rotational fishing is employed. At levels of fishing mortality well above F_{MAX}, rotational fishing does appear to modestly decrease the loss of yield-per-recruit due to incidental mortality. This decrease is due to the fact that incidental mortality, by somewhat lowering F_{MAX}, exacerbates the effects of overfishing, whereas rotation alleviates the loss of yield-per-recruit due to overfishing.

The effectiveness of sea scallop rotational fishing can be understood by examining fishing mortality at size for various rotational strategies. Figure 7 shows fishing mortality as a function of shell height for no rotation and for 3-, 6-, and 9-yr rotations for $F_{AVG} = 0.2$ (Fig. 8A), and $F_{AVG} = 0.6$ (Fig. 8B). Rotational fishing (especially for longer periods) tends to reduce the fishing mortality on small scallops and shift this effort onto larger individuals, thereby increasing yield-per-recruit, especially when overfishing is occurring. The periodic peaks in fishing mortality seen in the rotational strategies occur at the sizes where a new cohort begins to be fished (i.e. when the scallops are some integer number of years past their age at 40 mm). In practice, these peaks are likely to be much less pronounced because of variations in individual growth rates and settlement times. However, the qualitative pattern of increasing selectivity with size should not be affected by such variations.

Sea scallops are an ideal candidate for rotational management, combining fast growth and low natural mortality with a sedentary adult lifestyle. In addition, sea scallops are recruited into the fishery at a size that is well below optimal from a yield-per-recruit perspective. The increase in size-selectivity induced by rotation described above should therefore induce an increase in yield-per-recruit. However, in those fisheries where the size-at-entry to the fishery is much larger, rotation would not be expected to induce gains in maximal yield-per-recruit (see Fig. 5A). On the other hand, it appears that rotation increases biomass-per-recruit regardless of the size-selectivity of the fishery (Fig. 5B). Botsford et al. (1993) found that rotation increased biomass- but not yield-per-recruit for red sea urchins. These results are consistent with the above discussion because the minimum legal size for landing the urchins was already near-optimal.

Although the exact levels of yield- and biomass-per-recruit obtained with or without rotation are sensitive to such factors as natural mortality and growth rates, the relative gains of rotation over constant fishing are much less sensitive to these factors. Rotation will improve yield-per-recruit under a broad range of parameter choices provided that 1) the ratio of growth to mortality K/M is

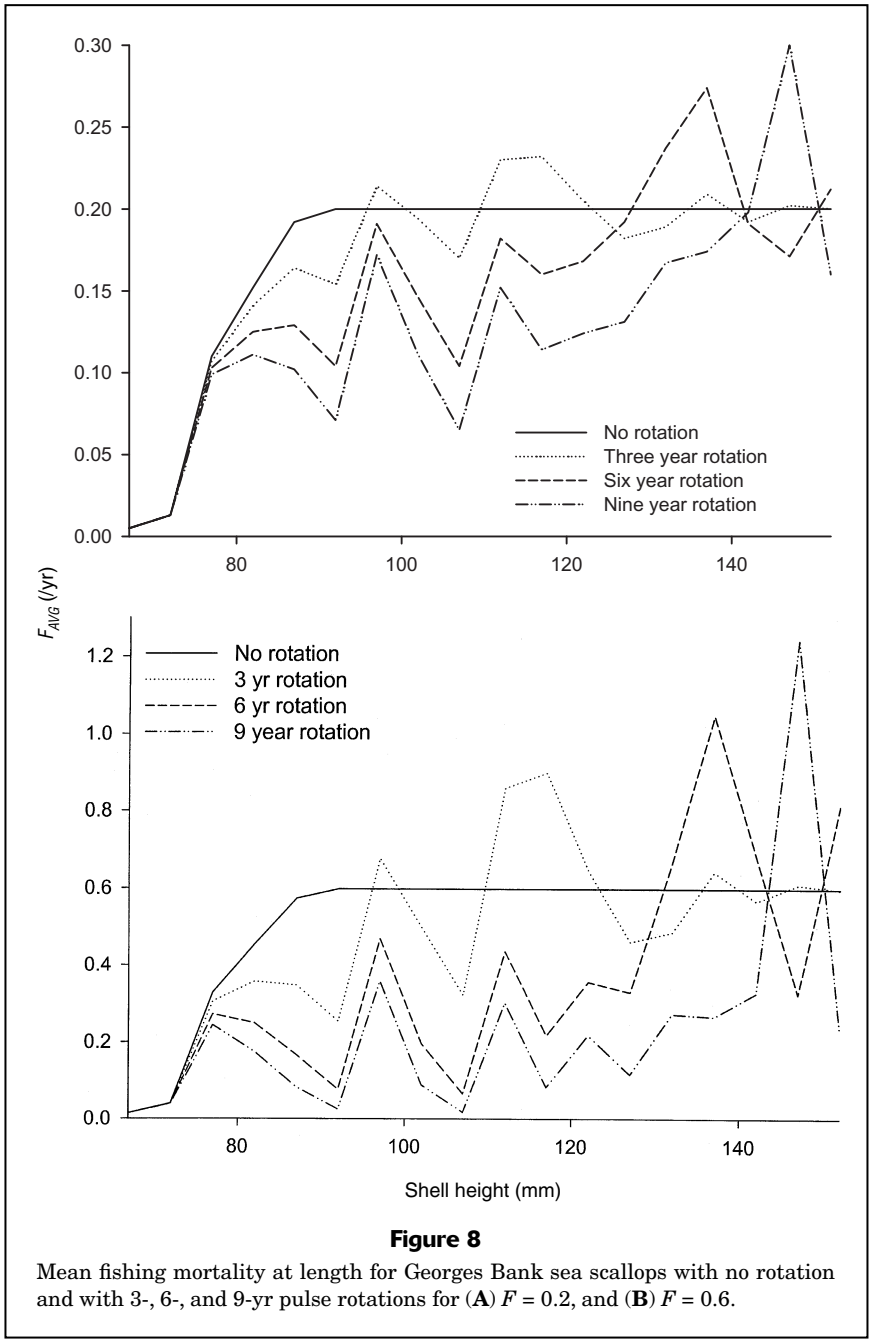

Figure 8

Mean fishing mortality at length for Georges Bank sea scallops with no rotation and with 3-, 6-, and 9-yr pulse rotations for (**A**) $F = 0.2$, and (**B**) $F = 0.6$.

sufficiently high (greater than about 0.5 with the other parameters in the model fixed as given in Table 1), and 2) size-selectivity is suboptimal. Rotation improves biomass-per-recruit under even a wider range of parameters.

Allee effects may occur in broadcast spawners such as urchins and scallops. Areas that are closed for several years may allow these animals to form dense aggregations (that would likely be heavily fished if not closed), thereby improving fertilization success (Botsford et al., 1993). Such an effect would mean that rotation could produce greater benefits in fecundity than would be suggested by biomass- or eggs-per-recruit curves.

Metapopulation structure might also be considered when designing a rotational strategy. If recruitment is limited by the supply of settling larva, an area that is a source of larva might be fished less than that required to maximize yield-per-recruit in order to increase larval supply (Tuck and Possingham, 1994).

The calculations that indicate long optimal rotational periods assume low constant natural mortality, independent of age or density, based on the study of Merrill and Posgay (1964). There is some evidence that the natural mortality rate of sea scallops may increase with age or size for shell heights greater than about 110 mm (Mac-

Donald and Thompson, 1986). If this is the case, optimal rotational periods would be shorter than calculated here, although the yield-per-recruit formalism would remain valid. More serious problems would be caused if there is density-dependent mortality of adults or if high adult densities inhibited recruitment because rotational closures can induce higher densities than would constant fishing. If either of these processes occur, shorter rotation periods would be advisable to minimize this problem. For sea scallops, however, observations of areas that have been closed to fishing for a number of years give no indication that such density-dependent processes are occurring (Fig. 2b in Hart 2001, and Table B5-8 in NEFSC[1]).

An extreme case of rotational fishing is true pulse fishing, where all exploitable individuals are removed at periodic intervals (see e.g. Sluczanowski, 1984). Thus, true pulse fishing corresponds to pulse rotation (as defined in the present study) with an infinite fishing mortality. Such pulse fishing is not optimal for sea scallops, as can be seen by the slight decline of yield-per-recruit at high fishing mortalities in Figure 1 because at very high fishing mortalities, the partial selectivity of the gear loses its effectiveness and all individuals that are even slightly selected to the gear (i.e. that are even slightly greater than $h_{\min}$) will be removed. To put it another way, at high fishing mortality rates, the additional (i.e. marginal) catch obtained from a further increase in F will disproportionately consist of small animals, thereby reducing yield-per-recruit. Pulse fishing would be optimal if knife-edge selectivity is assumed. For this reason, the assumption of knife-edge selectivity would lead to unrealistic results for cases such as sea scallops, where gear selectivity increases more gradually with size. Proper application of rotational theory therefore requires a careful examination of fishing selectivity with size.

Pulse fishing can be related to the classic Faustmann theory of forest rotation (see e.g. Reed, 1986; Clark, 1990). In this theory, if a stand of trees in an area that has last been harvested t years previously has value $V(t)$, then the optimal time to harvest the trees satisfies

$$V'(t) = \delta\big(V(t) - c\big) + \delta \frac{V(t) - c}{\exp(\delta t) - 1}, \qquad (6)$$

where δ = the discount rate; and
c = the cost of harvesting.

In the case of a fishery, $V(t)$ would represent the expected value of the exploitable stock (e.g. those of shell height greater than $h_{\min}$) at time t. (Note that in this context, unlike the original forest application, it is not necessary to assume that all exploitable individuals are the same age.) In the case of scallops, assuming all scallops command the same price per unit weight, $c = 0$, and $\delta = 0.1$, this formula would give an optimal rotation period of about 6.1 years (the optimal period would be moderately longer for realistic positive values of c). This value corresponds well to the rotation time of 6 years that optimizes discounted yield-per-recruit (see Fig. 2). However, the yield-per-recruit for 6-yr pulse fishing, $V(6)$, is less than 80% of the maximal yield-per-recruit obtained by fishing uniformly. Again, the reduced yield-per-recruit is due to the fact that pulse fishing induces knife-edge selectivity at $h_{\min}$, rather than the usual gradual increase in vulnerability to the gear.

Symmetric rotational strategies appear to give less benefit than does pulse rotation. However, optimal pulse rotation would require high, and possibly impractical, levels of effort in an area when it is opened (e.g. F of about 1.7 for a 6-yr pulse rotation). In addition, such a strategy would require that areas be closed most of the time, possibly inducing social-economic disruptions by closing traditional fishing grounds for long periods. Compared to pulse rotation, symmetric rotation requires less concentrated effort, allows areas to be open half the time, and is less sensitive to the assumption of constant natural mortality. One possible compromise between pulse and symmetric rotation is to close an area for half the time and then gradually increase effort during the opening. For example, an area might be closed for three years and then fished for the next three years at F_{MAX}, $2F_{\mathrm{MAX}}$, and $3F_{\mathrm{MAX}}$, respectively.

Questions have been raised regarding the appropriateness of the use of whole-stock fishing mortalities as targets or reference points for fisheries of sedentary stocks that include rotational or long-term closures (or both) (NEFSC[2]). The solid line in Figure 9 gives the whole stock (biomass-weighted) fishing mortality (assuming constant recruitment everywhere) for a pulse rotational system consisting of six areas, one of which is fished each year in turn. This whole-stock fishing mortality was obtained by simply dividing the yield-per-recruit for a 6-yr pulse rotation by the corresponding biomass-per-recruit. The x axis is F_{AVG}, which should be proportional to true effort. As can be seen, whole-stock fishing mortality is proportional to effort for low fishing mortalities, but then flattens to a maximum of just under 0.4.

A similar situation can happen even if an area is fished uniformly, except that a portion of the area is set aside as an indefinite closure. The dashed line in Figure 9 gives an example for the case when 10% of the area is permanently closed and is allowed to equilibrate to the biomass-per-recruit corresponding to zero fishing mortality. Whole-stock fishing mortality shows a relationship to the actual fishing effort (the fishing effort in the open area only) in the open areas that is similar to that of rotational fishing. In both cases, closed area biomass dominates the whole-stock fishing mortality calculation at high fishing effort. The yield at high fishing effort is essentially derived from incoming recruitment, which is not sensitive to fishing effort for very high effort levels. Therefore, the whole-stock fishing mortality becomes nearly constant when effort is high.

[2] NEFSC (Northeast Fisheries Science Center). 1999. Report of the 29th northeast regional stock assessment workshop (29th SAW). Stock Assessment Review Committee (SARC) consensus summary of assessments. NEFSC Ref. Doc. 99-14, 347 p. [Available from NEFSC, 166 Water St., Woods Hole, MA 02543.]

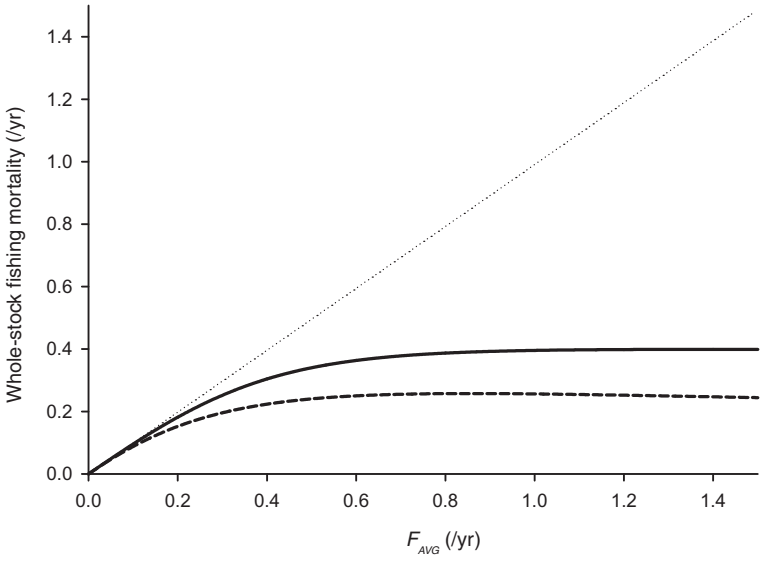

Figure 9

Whole-stock fishing mortality as a function of effort (F_{AVG}) for sea scallops with a 6-yr pulse rotation (solid line), and constant fishing with 10% of the area permanently closed (dashed line). The dotted line is the line $y = x$.

The current situation for sea scallops in Georges Bank gives an even more extreme example of this phenomenon. About 80% of the biomass lies in the groundfish areas that have been closed to scallop fishing for most of the time since December 1994. Because these areas will be closed to scalloping in 2002, the whole-stock fishing mortality in this year cannot exceed the F_{MAX} reference point of 0.24. Therefore, according to the current overfishing definition (the whole-stock F is below F_{MAX}), the stock cannot be overfished. Nonetheless, the fishing mortality in the open areas may exceed F_{MAX}, resulting in growth overfishing in these areas. Thus, the stock in the open areas could be overfished from a yield-per-recruit perspective even if the whole-stock F is below F_{MAX}.

The opposite situation could also occur. If scallops in the groundfish closed areas on Georges Bank were fished more than slightly above the $F_{\mathrm{MAX}} = 0.24$ reference point, the whole-stock fishing mortality would also be above this reference point and overfishing would be considered to be occurring. However, an area that has been closed for a number of years should be fished harder, compared to an area that has never been closed, once the area is reopened in order to maximize yield-per-recruit. Thus, a strategy that would maximize yield-per-recruit might require a whole-stock F that would in some years be higher, and in some years lower, than the conventional overfishing reference point.

A whole-stock fishing mortality rate may therefore not be the most appropriate metric for overfishing definitions when some areas are temporarily or permanently closed to fishing. Its value may not be representative of the yield-per-recruit that could be obtained at that level of fishing mortality. Furthermore, when most of the biomass is in closed areas, estimated whole-stock fishing mortality may be more sensitive to variations in recruitment and measurement error than to actual changes in effort.

As an alternative to a whole-stock fishing mortality metric, the following considerations are suggested for a fishing effort measure that is compatible with yield-per-recruit calculations. (1) Stock from areas that are not fished in a given time period should not be included in the fishing mortality calculation for that time period. In a relatively sedentary stock, the amount of biomass in the closed areas is irrelevant in determining the yield-per-recruit that will be obtained from the stock in the open areas. (2) Time-averaging of fishing mortality in the open areas is required to take into account the previous fishing history of the area. An area that has been closed for a number of years needs to be fished harder once opened than an area that has been continuously fished in order to maximize yield-per-recruit.

Based on these considerations, the time-averaged fishing mortality computed from the open areas only, F_{AVG}, is an appropriate measure of fishing mortality in fisheries managed by using rotational or indefinite closures. It is natural to take the averaging period equal to the rotational period p. With this metric, F_{MAX} is only slightly sensitive to the rotational period p and completely insensitive to the level of closed area biomass. Indeed, even if no closures existed, but fishing effort varied with time, it may still be advisable to employ a time-averaged fishing mortality because the previous history of fishing mortalities strongly affects the level of effort required to maximize future yield-per-recruit. If an area has been fished harder than F_{MAX} for a number of years, so that the population

size-structure in this area is smaller than the equilibrium size-structure obtained by fishing at F_{MAX}, then fishing the next year at a level somewhat below F_{MAX} will improve long term yield-per-recruit. Similarly, if an area has been fished below F_{MAX}, so that its size structure is larger than what would occur when fishing at a constant rate of F_{MAX}, then it may be optimal to temporarily fish at a level higher than F_{MAX}.

In summary, rotational fishing can improve yield- and biomass-per-recruit for long-lived sedentary stocks such as sea scallops. Rotational management can be part of a precautionary strategy because it can help alleviate the effects of growth and recruitment overfishing. Rotational management will however require a rethinking of conventional yield-per-recruit reference points.

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Appendix

Basic yield-per-recruit model

This appendix describes the basic yield-per-recruit model used for a cohort. In this model, recruits start at a specified shell height (or length) h_0. The shell height is converted into a starting age a_0 by using a von Bertalanffy growth equation. The shell height at time t is also obtained by using the von Bertalanffy growth curve. The shell height is converted into a meat weight by using a shell-height/meat weight formula:

$$w = \exp(a + b \ln(h)), \tag{7}$$

where w and h are in units of grams and millimeters, respectively.

Natural mortality occurs at a rate M, assumed for these simulations to be constant for all ages (M=0.1). The fishing mortality rate $F(h)$ on a scallop of shell height h is given by $F(h) = F_0 J(h)$, where F_0 is the fully recruited fishing mortality rate and $J(h)$ is the selectivity of the gear. $J(h)$ was taken to be 0 if h is less than a minimum shell height h_{min}, 1 if h is greater than a fully recruited threshold size h_{full}, and interpolated linearly as

$$J(h) = \frac{h - h_{\min}}{H_{\text{full}} - h_{\min}} \tag{8}$$

if $h_{\min} < h < h_{\text{full}}$. Individuals that are caught by the gear but are smaller than a maximum cull size h_d, are discarded and are subject to a discard mortality d. In these simulations, d is taken to be 0.2 (DuPaul[3]); however, the results are not very sensitive to the exact value of this parameter. All individuals caught at a size greater than h_d are assumed to be landed and are included in the total yield. $F_c(h)$ denotes the rate at which scallops of shell height h are caught and retained (i.e. not discarded).

The possibility has been raised that some scallops may be killed but not captured by the gear (Caddy, 1973; Myers et al. 2000). Caddy (1973) estimated that 15–20% of the scallops remaining on the bottom in the path of a scallop dredge are killed but not captured by the dredge. Murawski and Serchuk[4] estimated that less than 5% of the scallops remaining in the path of the dredge suffered incidental (noncatch) mortality. In order to use the above studies to estimate the relationship between incidental fishing mortality F_{I} and the fully recruited capture fishing mortality rate F_0, it is necessary to know the efficiency e of the dredge on a fully recruited individual. Denote by i the fraction of scallops that suffer mortality among those that were in the path of the dredge but that were not caught, so that i is estimated at 0.15–0.2 by Caddy (1973), and less than 0.05 by Murawski and Serchuk.[3] The ratio R of fully recruited scallops in the path of the dredge that are caught to those killed but not caught is

$$R = e / [i(1–e)]. \tag{9}$$

If fully recruited scallops suffer capture fishing mortality at rate F_0, then the rate of incidental fishing mortality will be

$$F_{\text{I}} = F_0 \ / \ R = F_0 \, i \, (1 - e) / e. \tag{10}$$

If e is taken as 50% (estimated as the average scallop dredge efficiency on Georges Bank[5]), then F_{I} would be in the range 0.15 F_0 to 0.2 F_0 according to Caddy (1973) and less than 0.05 F_0 according to Murawski and Serchuk.[3] To ascertain the effects of incidental fishing mortality on the yield-per-recruit calculations, model runs were performed with no incidental mortality, and also when F_{I} = 0.15 F_0; incidental fishing morality was applied to all size groups.

Let $Z(h)$ be the total mortality rate at shell height h (i.e. the sum of natural mortality, and discard, indirect, and landed fishing mortality). Then the fraction of recruits remaining t years after the beginning of the simulation is

$$S(t) = \exp\left(-\int_{a_0}^{t} Z(\tau) d\tau \right). \tag{11}$$

Total yield- and biomass-per-recruit are calculated by the formulas:

$$Y = \int_{a_0}^{a_f} S(t) F_c\big(h(t)\big) w\big(h(t)\big) dt \tag{12}$$

$$B = \int_{a_0}^{a_f} S(t) w\big(h(t)\big) dt, \tag{13}$$

where a_f = the ending age of the simulation, taken to be $30 + a_0$.

For convenience in these simulations, a_0 is taken to be 2 years; this age is assumed to correspond to a shell height of precisely 40 mm. In the rotational simulations reported in this study, the fully recruited landed fishing mortalities $F_c(h)$ (h>h_{full}) are assumed to vary periodically and are given in year k by F_{j+k}, where j is the year that the cohort reaches the starting age a_0.

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